NEW SPECIMENS OF LOWER JURASSIC HOLOSTEAN FISHES FROM INDIA

by S. L. JAIN

ABSTRACT. An account is given of new, well-preserved, deep-bodied holostean fishes (family Semionotidae) from the continental Lower Jurassic, India. A new genus, *Paradapedium*, has been erected with *Dapedium egertoni* Sykes 1853 as type-species. New specimens are assigned to *P. egertoni*. The validity of *Tetragonolepis oldhami* Egerton 1878 is supported but *T. analis* and *T. rugosus* are found to be indeterminable. The age and distribution of deepbodied semionotids is discussed. The evidence from the fossil fishes is in favour of a Liassic age for the Kota Formation. Knowledge of freshwater actinopterygians is improved.

It has been pointed out by Romer (1968, p. 242) that there is a major lacuna in our knowledge of fish evolution in the Jurassic. There is a wealth of Jurassic fishes, but nearly all are marine forms, and understanding of actinopterygian evolution is, therefore, an unbalanced one. Romer also wondered whether the freshwaters of Jurassic times were relatively destitute of actinopterygians. This paper may help to restore the balance in our understanding of fish evolution during the Jurassic, for it is concerned with certain members of a freshwater fauna of actinopterygian fishes from the Lower Jurassic Kota formation of India. The Kota formation is a member of the continental Gondwana Group, and occurs in the region of the Pranhita Godavari valley. King (1881) and Pascoe (1959, p. 987) have given an account of the geology, fauna, and flora of the Kota formation, to which must be added the discovery of dinosaur remains (Jain *et al.* 1962) about 20 feet below a fish-bearing Kota limestone. The study of the Kota fish is part of a programme of research on the rocks and fossils of the Pranhita Godavari valley by the Geological Studies Unit of the Indian Statistical Institute.

Three genera of semionotids, *Dapedium*, *Tetragonolepis*, and *Lepidotes*, are known from the Kota formation. These are all well-known members of the European marine fauna of Lower Jurassic age, and the significance of their occurrence in the freshwater Kota formation will be discussed later. Neither a fresh collection nor a critical study of the fish fauna from the Kota formation has been undertaken since Sykes (1851) proposed *Lepidotes deccanensis*, and Bell (1853) reported the boring at Kota, in which Sykes proposed *Dapedium egertoni*, and the subsequent description of material (5 species of *Lepidotes*, 1 species of *Dapedium*, and 3 species of *Tetragonolepis*) by Egerton (1851, 1854, and 1878). A study of *Lepidotes* based on restudy of type material and an examination of fresh collections has been completed (Jain, S. L. and Robinson, P. L.) and is awaiting publication. This paper is confined to the deep-bodied semionotids, *Dapedium* and *Tetragonolepis*.

Woodward (1895, p. 153) cast doubt on the validity of *Dapedium egertoni* Sykes 1853 by including it in the list of species based on fragmentary material. He (1895, pp. 161–162) recognized only one species of *Tetragonolepis* (*T. oldhami*) out of three proposed by Egerton. Pascoe (1959, p. 987), while listing the fauna and flora of the Kota formation, preferred not to alter the proposals of Sykes and Egerton. Menon

(1959) compiled a catalogue of Indian fossil fishes, keeping the original nomenclature, and did not comment on the validity of any taxonomic unit. Jain (1959) reported a fresh collection of fossil fish material from the Kota formation in 1958, and new specimens have been collected by field parties of the GSU, ISI, Calcutta, from the spring of 1958 to the winter of 1969-1970. Completion of this paper was postponed in the hope that additional good material would be found. It is disappointing that a ten-year period has yielded only 6 specimens of deep-bodied semionotids which could give some reliable information on the skull. Some of these specimens also have reasonably well-preserved body and fins. The number of fragmentary specimens however, is considerable. In general, it has been noticed that there is a scarcity of material of deep-bodied semionotids as compared with the lanceolate *Lepidotes*, the latter being by far the most abundant member of the fauna, though often represented by fragments.

The new specimens described here are preserved in the Palaeontological collections of the GSU, ISI, Calcutta. The specimens in the Geological Survey of India, Calcutta, and the British Museum (Natural History), London, are referred to as GSI and BMNH, respectively. A plaster cast of ISI P. 32 (Pl. 12) and of the hinder part of ISI P. 33 (Pl. 13—the anterior fitting part shown in the plate was not found at the time when the cast was made) have been deposited with the British Museum (Natural History).

'DAPEDIUM' EGERTONI Sykes

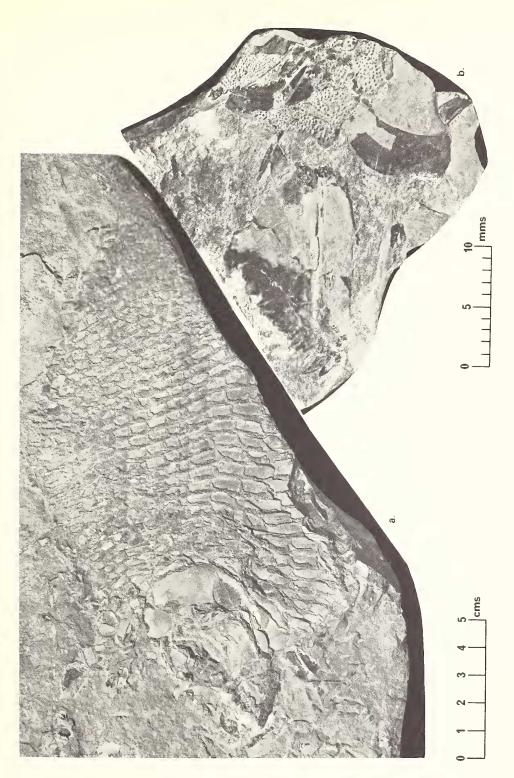
Generic name. In the early years of work on deep-bodied semionotids various generic names were used, as the distinguishing characters of these forms, and even their distinction from pycnodonts was still not clearly appreciated. So although the Indian form was first referred to by the name *Dapedius egertoni* Sykes (in Bell 1853) it was also termed *Tetragonolepis* or *Aechmodus* by Egerton (1851, 1854). By 1878, however, Egerton had recognized the Kota species as belonging to *Dapedius*. But he used the form of this generic name given by Agassiz in 1835, as did Sykes (in Bell 1853); however, the correct form is *Dapedium* Leach 1822 (see Gardiner, 1960, p. 299, and Woodward 1895, p. 128, for synonymy). The correct form of the generic name will be used in the next, historical, section of the paper.

The problem of the holotype. There is, at present, no clearly designated holotype of this species. It is necessary to review the early history of research on this fossil fish in order to make a proper choice of a specimen as lectotype.

The first mention of the species *Dapedium egertoni* is in a paper by Bell (1853). The paper gave an account of a boring near the village of Kota (spelt Kotah) put down in the Kota formation, which was situated a few miles north of the confluence of the rivers Pranhita and Godavari, on the left bank of the Pranhita. Mention is made of a specimen of a fossil fish, found in a loose mass of limestone slabs on the bank of the Pranhita River. This was a new species of *Dapedium*, differing from other species in the ornamentation of the scales, which Sykes named *Dapedium egertoni*. Neither illustration nor any proper description was given in Bell's paper, nor was the specimen referred to any collection. The specimen was, however, undoubtedly housed in the collection of the Geological Society of London, whose specimens were not individually numbered. Later in 1853 Sykes presented two more specimens of *D. egertoni* from Kota to the Geological Society of London. These two specimens were described and figured by Egerton in 1878.

EXPLANATION OF PLATE 10

Paradapedium egertoni. a. Lectotype, BMNH P. 12147a; b. BMNH P. 12146, lower jaw and some imperfect head bones. Photographs by British Museum (Natural History).



JAIN, Jurassic fish from India

Egerton made it clear that he was describing additional specimens of the species, which he was referring to *D. egertoni*; he was not describing Sykes's original specimen, nor was he formally designating a holotype.

In 1911 the Geological Society's collection of foreign fossils was presented to the British Museum (Natural History), and the Kota specimens were given individual catalogue numbers for the first time. 4 specimens were catalogued as *Dapedium egertoni*.

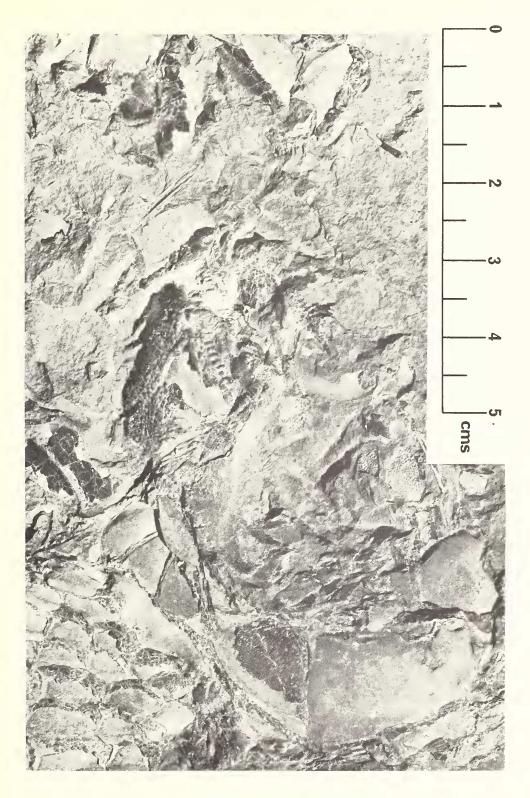
BMNH	P. 12146	not figured or described lower jaw and some imperfect cranial bones (this paper, Pl. 10).
counterparts	P. 12147	figured and described by Egerton (1878, pp. 6–8, and Pl. 11, figs. 4, 5) anterior part of the body, imperfect pectoral fin, opercular bones and one or two imperfect cranial bones.
of the same { individual	P. 12147 <i>a</i>	not figured or described dorsal part of the body, and a portion of the flank, opercular bones, lower jaws and part of head (this paper, Pls. 10, 11).
	P. 12148	figured and described by Egerton (1878, pp. 6-8, and Pl. 12, fig. 3) dorsal part of the body and imperfect dorsal fin.

It remains to try to discover which of the two undescribed specimens might be the original one mentioned in Bell's paper (1853), discussed by Egerton in that paper, and proposed as *D. egertoni* by Sykes. It is unlikely that the original specimen was P. 12146, as this is only a fragment, showing a lower jaw and some fragments of head bones; it does not show body scales, and the latter were mentioned by Egerton (in Bell, 1853), as having ornament rather different from that of other species of *Dapedium*. It is likely that the original specimen was P. 12147*a*, as this shows part of the head, and the anterior portion of the body of the fish. It is also the best of the 4 specimens collected in the nineteenth century and listed above. Thus this specimen is chosen as a lectotype, together with its counterpart P. 12147, for *Dapedium egertoni* Sykes. P. 12146 and P. 12148 are topotypes, referred to *D. egertoni*.

Description of the lectotype (BMNH P. 12147 and a). P. 12147 is a fragment (Egerton 1878, pl. 11, figs. 4, 5) being part of the counterpart of BMNH P. 12147a (described next). The specimen exhibits the anterior portion of the left-hand side of the body and a portion of the opercular apparatus. The scales have the usual peg-and-socket arrangement and those below the lateral line canal are deeper dorso-ventrally than those above. The scale rows are imperfect and no count is possible. The anterior end of the lateral line canal meets the operculum at about the middle of its length. The pectoral fin is represented by a faint impression of fin rays near the posterior edge of the subopercular. Opercular and subopercular are seen mesially partly as bone and partly as impressions. The opercular is deeper than the subopercular. The opercular process for articulation with the hyomandibular is set quite high on the former bone, and is situated a little below its upper margin. No other element of the opercular apparatus can be recognized with certainty. Situated next to the opercular, dorsally, is a bone which is probably the dermopterotic, and which is exposed in mesial view, partly as an impression of the external surface and partly as bone. The impression indicates that the external surface of the bone was tuberculated and mesially smooth. BMNH P. 12147a is mostly preserved as an impression on buff limestone, of which the ventral and posterior one-third of the body and tail is missing (Pl. 10, fig. a). The left-hand side of the fish is exposed in mesial view and displays

EXPLANATION OF PLATE 11

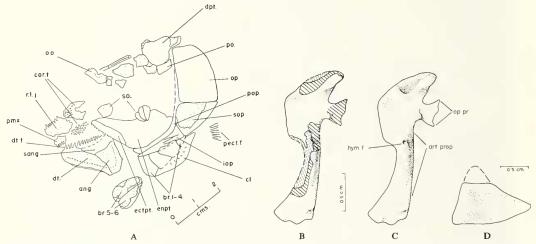
Paradapedium egertoni, lectotype (BMNH P. 12147*a*), details of the anterior portion. Photograph by British Museum (Natural History).



JAIN, Jurassic fish from India

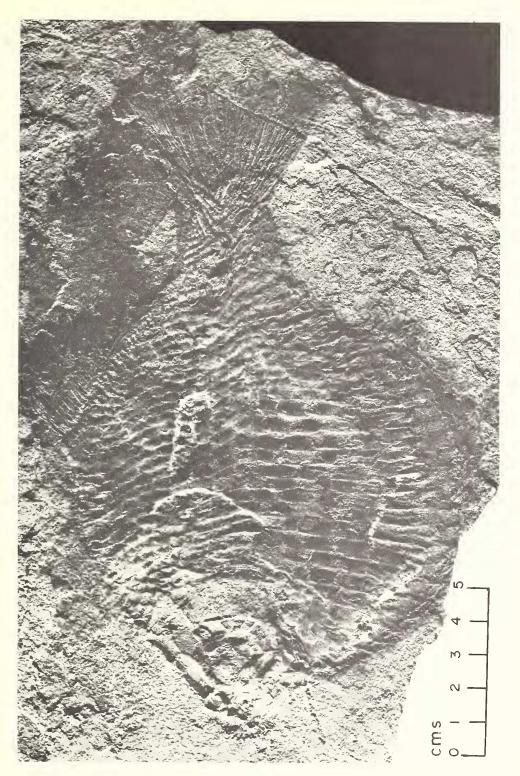
the opercular apparatus, branchiostegal rays, jaws, a part of the cheek region, and an indication of the roof of the skull. Nearly two-thirds of the anterior dorsal part of the body is preserved, with well-marked scale rows. The specimen is about 19.5 cms long, and 9 cms deep in the region of opercular apparatus.

The only membrane bone discernible in the skull is the dermopterotic. A number of suborbitals, which are displaced from their normal position (text-fig. 1A) are also seen. The dermopterotic is large and preserved mostly as an impression of the external surface, bearing fine tuberculations. There is no clear evidence of extrascapulars. A portion of the maxilla is seen lying anterior to the lower jaw (not seen in text-fig. 1 but discernible in Pl. 11), bearing 9 stout pointed teeth. It appears that



TEXT-FIG. 1. *Dapedium egertoni*, lectotype, BMNH P. 12147a. A, Anterior portion; B, hyomandibular (crushed bone hatched, impressions of bone on matrix broken hatched); c, restoration of hyomandibular; D, quadrate.

the posterior one-third of the maxilla is broken off. A disarticulated fragment bearing 5 downwardly directed teeth is probably left premaxilla (text-fig. 1A). The palatopterygoid arch is well displayed and appears to be quite stout. The ectopterygoid bears 14 fine, pointed teeth and is firmly ankylosed to the entopterygoid. The hyomandibular (text-fig. 1B and C) is displaced and is observed in one corner of the slab. It is elongated, with a slender arm ventrally and a laterally expanded portion dorsally. It is partly damaged but the impressions allow fair evidence of its shape. The bone is crushed at the site of the hyomandibular foramen, which is set obliquely, at about mid length. The edge of the hyomandibular arm is clearly demarcated by a vertical depression for the overlap of the left preopercular. The dorsal part of the hyomandibular is rather delicate and obliquely expanded with a well-defined opercular process. The quadrate (text-fig. 1D) can be recognized in the dissociated elements.



JAIN, Jurassic fish from India

It has a somewhat triangular shape, allowing for the restoration of the dorsal part which is partly crushed. The articulation facet is not pronounced.

The lower jaw (text-fig. 1A) of the left-hand side is in association. The external bones are partly preserved here, revealing fine tuberculations on dentary and angular. The mandibular sensory canal is also visible. The marginal dentary teeth are well preserved but the most anterior are probably missing. The teeth are uniformly sharp, pointed, and decrease in size posteriorly. 13 teeth are preserved. There are 2 clusters of teeth (Pl. 11 and text-fig. 1A), dorsal to the mandible, the top of most of which is gone. The cluster next to the mandible seems to be coronoid teeth, and the cluster dorsal to it is probably made up of prearticular teeth. The opercular apparatus is complete, and the shape of its various elements can be determined in P. 12147 and a. The opercular is deep, somewhat rectangular, narrow dorsally, and wider ventrally. The proportion of width to length is approximately 1:2. The subopercular is about half as deep as the operculum. The interopercular is partly crushed and partly hidden by the preopercular. The form of the preopercular can be worked out from impressions and is shaped like an open L. The tuberculations on the bones of the opercular apparatus seem to be very fine. Four branchiostegal rays, with damaged distal ends, are present next to the interopercular. Close to them are to be seen another 2 branchiostegal rays. Thus there are at least 6 small branchiostegal rays. The cleithrum is arched. Its upper extremity lies somewhere near the middle of the subopercular and the lower extremity lies near the last associated branchiostegal rays (text-fig. 1A).

The trunk in P. 12147*a* is imperfect and all fins, except the pectoral, are wanting. The preserved two-thirds portion of the body shows that it was laterally compressed and deeply fusiform. The scales have a broad peg-and-socket articulation, but no sharply thickened rib is present on the inner face. The scales above the lateral line canal do not appear to be as elongate as the ones below and those of the flank region are even more elongate. The dorsal and ventral ridge of the body is imperfect, which renders the number of scale rows indeterminable, but it appears that there were at least 8 to 10 horizontal rows of scales on either side of the lateral line canal. The pectoral fin is approximately as high on the body as in species of *Dapedium*. Only the bases of the fin rays are preserved, of which 10–11 can be counted.

SYSTEMATIC DESCRIPTION

Infraclass Holostei Order semionotiformes Suborder semionotoidei Family semionotidae

Paradapedium gen. nov.

Type species: Dapedium egertoni Sykes 1853.

Diagnosis. Semionotids having abdominal region protuberant ventrally; head small in relation to the body. Postrostral absent. Mandible short, deep, with coronoid elevation and anterior tooth enlarged. Teeth slender and pointed. Suborbitals, 9-10, extending beyond middle of orbit. Circumorbitals probably 15-16. Cleithrum arched; suprascapular large, triangular. Extrascapulars, 3. Branchiostegal rays 6, small and inconspicuous. Hyomandibular slender, elongated; hyomandibular foramen at about mid length. No ossification around notochord. Neural spine fused to neural arches throughout the length of the body. Dorsal fin arising from about the middle of the back and extending to about the tail, has about 35 lepidotrichia. Anal fin shorter, opposed to hinder end of dorsal, has about 25 lepidotrichia. All lepidotrichia distally segmented and bifurcated and all fins with supporting fulcral rays. Complete squamation over trunk; flank and belly scales elongated dorso-ventrally. Dorsal ridge scales conspicuous, pectinate, or slightly denticulate. Ventral ridge scales slightly more conspicuous than dorsal, usually delicately pectinate.

Distribution. Lower Jurassic, India: Kota formation.

Paradapedium egertoni (Sykes) emended herein

Plates 10-14; text-figs. 3-6

Synonym. Dapedium egertoni Sykes 1853.

Occurrence. Kota Formation, India. A geological map of the Pranhita–Godavari Valley is given by King (1881). Fossil localities in the Kota formation are shown in text-fig. 2.

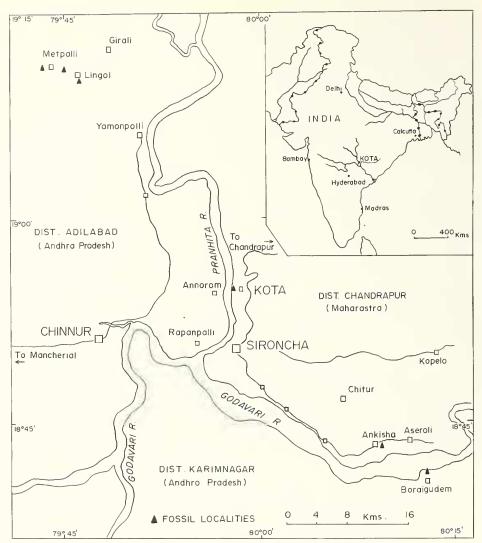
Material. Lectotype, in counterpart, BMNH P. 12147 and a, Kota formation, India, about 19.5 cm, fish wanting skull and tail.

Other specimens. BMNH P. 12146 and 12148, Kota formation, India; both fragmentary but the former displays left lower jaw and some imperfect head bones, mainly as impressions and the latter displays dorsal part of the body with imperfect dorsal fin.

New specimeus. ISI P. 32, Kota ledge, Kota formation, nearly complete fish, approx. 19.5 cm long; ISI P. 33, Kota ledge, Kota formation, nearly complete fish, approx. 25.5 cm long; ISI P. 34, near village Ankisha, Kota formation, nearly complete fish, approx. 25 cm long; ISI P. 35, near village Boraigudem, Kota formation, fish wanting anterior part of head and posterior fins, approx. 14.5 cm long. All fossil localities are shown in text-fig. 2.

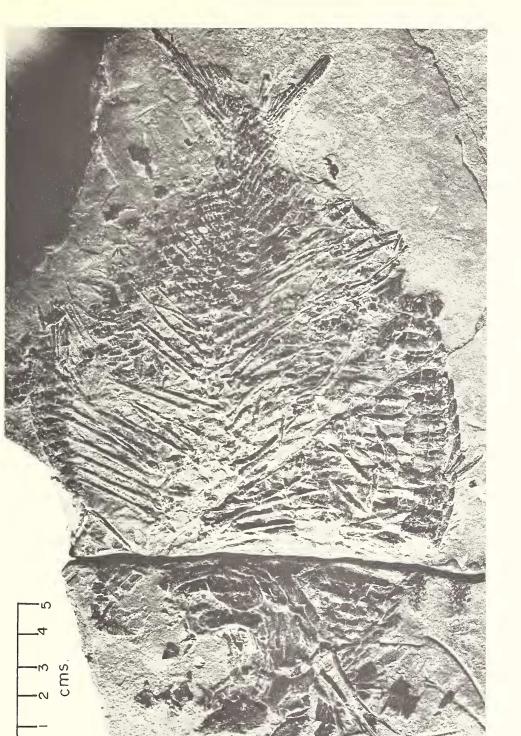
Diagnosis of species. Same as for the genus.

Description. Paradapedium egertoni is a moderately large semionotid reaching 200–320 mm in length and 120–195 mm in depth. Approximate depth/length ratio of the fish is about 1:1.6 to 1:1.7 (ISI P. 32, 34). The shape of the body is clearly hypsisomid and the whole body is covered with scales. The head region is rather small, deepened with a tendency of co-ossification of dermal roofing elements in larger specimens (ISI P. 34). The basicranial axis is not bent upwards. The frontal, parietal, and dermopterotic are differentiated by clear sutures in ISI P. 32 (text-fig. 3B). Although the course of the lateral line canals of the skull is impossible to make out, the anterior and middle pit lines on the parietal are conspicuous. The dermopterotic



TEXT-FIG. 2. Map showing fossil localities in the Kota formation. Inset: outline map of India showing the village Kota and tributaries of the river Godavari.

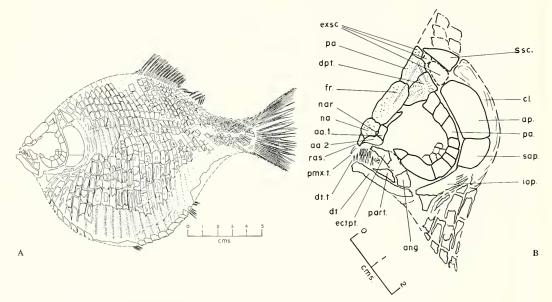
is somewhat larger than the parietal. The suprascapular is large and triangular. All skull roofing bones bear fine tuberculations. There are three extrascapulars, two smaller ones adjacent to the parietal, followed by the most ventral, which is also the largest. The orbit is reasonably well defined (ISI P. 32 and 35) and is moderate in size. The circumorbital series is best observed in ISI P. 35 (text-fig. 5B) where 5 bones



JAIN, Jurassic fish from India

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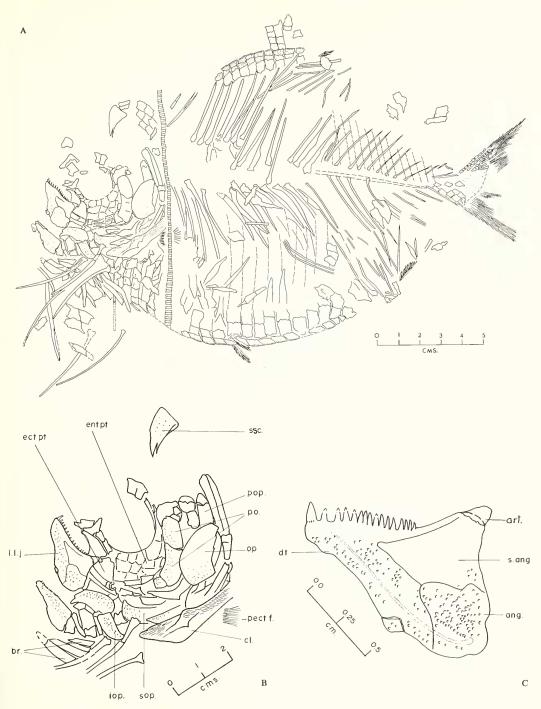
are preserved and another four are indicated by impressions. All circumorbitals are small and it seems there may have been at least 15–16 of them surrounding the orbit. The suborbitals are displayed well in ISI P. 32 (text-fig. 3B) and 35 (text-fig. 5B). These form in an arched series, varying in size, nine in ISI P. 32 and ten in ISI P. 35. The snout pattern is reasonably well defined in ISI P. 32 (text-fig. 3B). The rostral is a small element and abuts against the large nasals. The post-rostral is absent. An anterior and posterior antorbital can be recognized. The nasal aperture is single as in *Dapedium* and *Lepidotes* (Gardiner 1963). The palate is exposed in ISI P. 33 and even though the bone is crushed it is fairly easy to distinguish the arch-like entopterygoid and metapterygoid. The ectopterygoid is not preserved completely in any



TEXT-FIG. 3. Paradapedium egertoni gen. nov., ISI P. 32. A, complete specimen; B, anterior portion.

specimen but in ISI P. 32 it is seen to be represented by a series of teeth and fragments of bone. The premaxilla is either missing or damaged. Three slender and pointed premaxillary teeth can be recognized in ISI P. 32 of which the most anterior is enlarged. Maxilla is missing from all specimens. The hyomandibular (fig. 1B and C) is elongated, with a slender arm ventrally and a laterally expanded portion dorsally, bearing the hyomandibular foramen (VII) at about mid length (BMNH P. 12147*a*). The quadrate is probably triangular with poorly defined articulation facet (BMNH P. 12147*a*).

The lower jaw is preserved in ISI P. 32, 33, and 34, as well as in BMNH P. 12146 (Pl. 10, fig. *b*). It is remarkably short and deep, with coronoid elevation, comprising distinct dentary, angular, and surangular elements. All the external bones bear coarse tuberculations (text-fig. 4c). The course of the mandibular canal can be clearly traced. There are 15–16 teeth on the dentary of which the most anterior is enlarged, giving a tusk-like appearance. The opercular apparatus is partly exposed in all



TEXT-FIG. 4. *Paradapedium egertoni* gen. nov., ISI P. 33. A, complete specimen; B, anterior portion. (Broken lines in entopterygoid are cracks in the bone, *not* sutures.) C, left lower jaw.

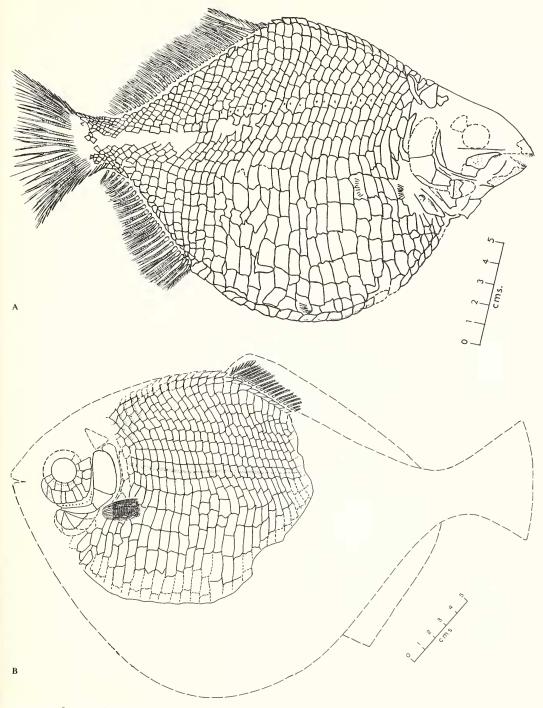
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specimens but it is best displayed in ISI P. 35 (text-fig. 5B). The preopercular is partially hidden in most specimens but has a clear ascending process. The opercular is deep and maintains the approximate proportions of length/width as 2:1. It forms a well-marked arched series with subopercular and interopercular. The cleithrum is arched. Four branchiostegal rays are preserved in ISI P. 33 (text-fig. 4) and ISI P. 35 (text-fig. 5B) but the lectotype displays 6 (text-fig. 1A). The whole body of the fish is covered with scales (Pl. 14 and text-fig. 5A), though in some specimens the scales are damaged. The scales ventrally to the lateral line canal are deeper than those in the dorsal region. A rib-like thickening is evidenced in the scales preserved ventrally to the lateral line canal, but is variable in development (ISI P. 33). Postcleithral scales are moderately enlarged (ISI P. 34). Dorsal and ventral ridge scales are a little more conspicuous than in *Dapedium*. Dorsal ridge scales are pectinate or slightly denticulate and ventral ridge scales are delicately pectinate (ISI P. 33, Pl. 13).

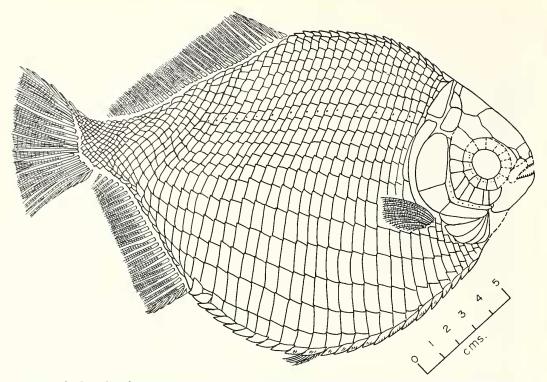
ISI P. 33 displays the axial skeleton as the scales have been leached out (text-fig. 4A and Pl. 13). The notochord must have been persistent as no traces of ossification have been detected. It occupied a position in which roughly one-third of the body lay above it and two-thirds below it. The bases of neural and haemal arches are moderately expanded and separated from each other. The neural and haemal spines are fused with their corresponding arches throughout the entire length of the body, unlike Dapedium where neural spines are fused only in the hinder half of the tail, but quite like Hemicalypterus. Median fins are best displayed in ISI P. 34 (text-fig. 5A and Pl. 14) but are partly visible in other specimens as well. The dorsal fin arises from the middle of the body and extends to nearly the end of the trunk, posteriorly. It has approximately 35 fin rays. Each fin ray is distally bifurcated and the leading fin ray has fringing fulcra. The anal fin is less extensive than the dorsal and its fin rays are more sparsely disposed. It has approximately 25 segmented and distally bifurcated rays, and the leading fin ray is provided with fringing fulcra. The caudal fin is well preserved in ISI P. 32 (Pl. 12) and ISI P. 34 (Pl. 14). It is hemiheterocercal and symmetrical and composed of about 22 segmented and distally bifurcated rays. There are fringing fulcra on both dorsal and ventral borders of the fin but these are less conspicuous ventrally than dorsally. The pectoral fin appears quite high on the flank, as in Dapedium. There were probably about a dozen fin rays of which nine are indicated (ISI P. 34, text-fig. 5B). The fin rays are segmented and distally bifurcated. The pelvic fin is rudimentary and is displayed in ISI P. 33 (Pl. 13). Only 2-3 fin rays can be recognized but the leading fin ray bears distinct basal fulcra.

A reconstruction of *Paradapedium egertoni* is given in text-fig. 6, based on the lectotype (BMNH P. 12147 and a) and ISI specimens (P. 32 to 35).

Discussion. All specimens assigned to *Paradapedium egertoni* have been obtained from localities in the Kota formation, India. The disposition of dermal bones, opercular apparatus, pointed non-tritoral teeth in the jaws, presence of conspicuous fulcra on all fins, and the extension of dorsal fin to not more than half the length of the trunk are some of the important characteristics shared by all specimens. The assessment of morphological uniformity is not always easy due to imperfection of some of the specimens collected in the nineteenth century, because of intraspecific



TEXT-FIG. 5. *Paradapedium egertoni* gen. nov., A, ISI P. 34, complete specimen; B, ISI P. 35, complete specimen with restored outlines.



TEXT-FIG. 6. Paradapedium egertoni gen. nov., reconstruction of complete fish from holotype (BMNH P. 12147 and a) and ISI specimens (P. 32 to 35).

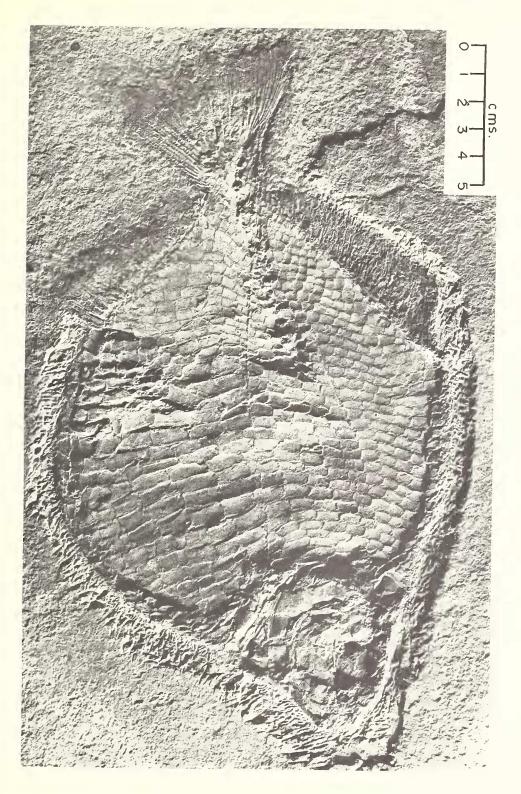
variation (e.g. number of suborbitals) and variations due to size (e.g. co-ossification of dermal bones of skull in larger specimens). A comparison shows a morphological uniformity which is consonant with their being individuals of a single species.

Paradapedium has closest affinities with *Dapedium*. It may, therefore, be useful to compare some important characteristics of the two. The body proportions of *Paradapedium* on 2 ISI specimens and *Dapedium* on 15 BMNH specimens were examined. Depth of the body below the lateral canal as percentage of total body depth was measured along the vertical line passing through lateral line canal at the point of maximum body depth:

	Depth below lateral line canal as percentage of total body depth
P. egertoni (ISI P. 32)	70%
P. egertoni (ISI P. 34)	71.9%
D. politum (BMNH: 6 specimens)	61-65.1%
D. colei (BMNH: 3 specimens)	61.9-65.5%
D. punctatum (BMNH: 3 specimens)	61.5-65.3%
D. dorsale (BMNH: 3 specimens)	60.2-64.9%

EXPLANATION OF PLATE 14

Paradapedium egertoni gen. nov., complete specimen, ISI P. 34, from Kota formation, India.



JAIN, Jurassic fish from India

The length of the head (from tip of the lower jaw to the posterior margin of the operculum) and depth of the head (from dorsal edge near the extrascapular to the ventral edge of the mandible) as percentage of the length of the fish (from the anterior tip of the lower jaw to the end of the body lobe) was measured on one complete specimen of *Paradapedium* (ISI) and 13 specimens of *Dapedium* (BMNH):

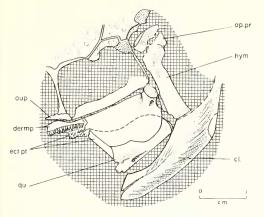
	Length of the head as percentage of length of the fish	Depth of the head as percentage of length of the fish
<i>P. egertoni</i> (ISI P. 34) <i>D. politum</i> (BMNH: 6 specimens)	15% 26·0-33·4%	16·3% 37·0-41·0% (5 specimens)
D. colei (BMNH: 4 specimens) D. punctatum (BMNH: 3 specimens)	29·5-34% 28·6-31·8%	33·3-40% 34·4-37·1%

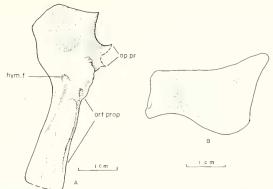
The lack of well-preserved specimens of *Paradapedium* stands in the way of determining range of head and body proportions. However, *Paradapedium* probably has a deeper body and smaller head than *Dapedium*.

The roofing bones of the skull are heavily ossified with heavy tuberculations in *Dapedium* but in *Paradapedium* they are not heavily ossified and bear fine tuberculations. The suborbitals are variable in number in *Paradapedium* (9–10) and *Dapedium* (6–11). The suborbitals extend beyond the mid orbit in *Paradapedium* but not in *Dapedium*. The extrascapulars in *Paradapedium* are not prominent; only one specimen shows three but in *Dapedium* these are very prominent and vary in number, 4–6 (Woodward 1895, Wenz 1967).

The hyomandibular of *Dapedium* has been briefly described by Woodward (1895) but not illustrated. A specimen of D. punctatum (BMNH 43435) exhibits the hyomandibular particularly well (text-fig. 8A). It is elongated and laterally compressed with considerable expansion above, but contracted in its lower half with nearly parallel anterior and posterior edges. The hyomandibular foramen is situated well dorsal to the mid length of the hyomandibular. Posteriorly there is an opercular process, lying in the same plane as the body of the bone. The posterior edge of the narrow ventral stem of the bone is slightly grooved for the reception of the anterior edge of the operculum. BMNH P. 4423 also shows the hyomandibular of Dapedium (text-fig. 7) but the dorsal half of the bone has been broken and crushed in, and the details are not seen so well. Nevertheless the 2 specimens suggest that the shape of the hyomandibular may be rather uniform in Dapedium. The hyomandibular of Paradapedium (text-fig. 1B and C) is narrower than that of Dapedium and dorsally it is much more expanded. The hyomandibular foramen is set more nearly in the middle of the bone, and the opercular process is clearly marked. The hyomandibulae of Dapedium and Paradapedium, therefore, differ from each other in several ways.

Symplectic and quadrate have been mentioned as 'unknown' in *Dapedium* by Woodward (1895) and Wenz (1967) does not describe either bone of that genus. BMNH 36883 (*D. punctatum*) exhibits lower jaw, palate, and quadrate and symplectic in association in mesial view (text-fig. 9). The symplectic is somewhat displaced but has a stout, expanded, and somewhat squarish portion anteriorly and a narrower portion posteriorly. The quadrate in *D. punctatum* as exhibited by BMNH 36883 (text-figs. 8 and 9) and *Dapedium* sp., BMNH P. 4423 (text-fig. 7) is rather





TEXT-FIG. 7. Dapedium sp. (BMNH P. 4423), left palatal complex, quadrate and hyomandibular.

TEXT-FIG. 8. *Dapedium punctatum*. A, hyomandibular from BMNH 43435; B, quadrate from BMNH P. 36883.

stout with a pronounced articular process. In BMNH P. 4423 (text-fig. 7) the quadrate is partly overlaid by the ectopterygoid but the curved border of the quadrate can be distinguished because flakes of the ectopterygoid have been broken away. The quadrate of *Paradapedium* (text-fig. 1D) is only partly known. It is not so stout and somewhat triangular in shape. The articulation facet is not pronounced. The symplectic of *Paradapedium* is unknown.

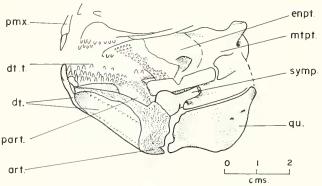
The lower jaw of *Dapedium* is well known and described by Woodward (1895) as remarkably short and deep, with coronoid elevation, comprising distinct dentary, splenial, articular, and probably coronoid elements. The mandible of *Paradapedium* is similar to *Dapedium* but the dentary in *Paradapedium* is more definitely V-shaped and in *Dapedium* it is more open V-shaped.

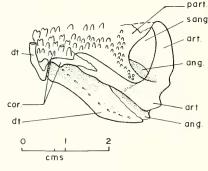
In Amia Meckel's cartilage is persistent and well chondrified, extending as an L-shaped structure, one 'arm' from the region of the jaw articulation to the symphysis, the other 'arm' from the region of the jaw articulation to the top of the coronoid process. It seems that in *Dapedium* this cartilage is ossified and can be called an 'articular' bone. The articular bone in *Dapedium* has exactly the shape of Meckel's cartilage in Amia (BMNH 36883: text-fig. 9; BMNH P. 4877: text-fig. 10). It extends dorsally to the coronoid process of the lower jaw. The articular is distinguishable from other dermal bones in being more 'crumpled' and less smooth. The articular is seen in external view of the lower jaw in *Dapedium* emerging to a variable degree in different specimens above and behind the surangular. In *Paradapedium* (text-fig. 4c) this feature seems to be similar.

BMNH 36883 (text-fig. 9), a right lower jaw seen in mesial view, shows that the symphysial facet in the lower jaw of *Dapedium* is contributed by three 'layers' of bone by individual subfacets. The dentary contribution is the most external with an elongate subfacet and crowned by the most anterior dentary tooth. A middle 'layer', with a distinct subfacet, lies sandwiched between dentary and coronoid. The mesio-dorsal coronoid 'layer' has its own rugose facets and well-developed teeth above. These three layers can be traced backwards along the jaw as separate

bones partly overlying one another. Reconstruction of the lower jaw of *Dapedium* has been attempted in three stages (text-fig. 11) from BMNH P. 4877. The dentition in *Dapedium* is variable. A few species have bifid or mammiliform apex and others have styliform teeth with simple apex. In *Paradapedium* the teeth are slender, elongated, and pointed and the most anterior tooth of the dentary is enlarged. The opercular apparatus and cleithrum are more or less similar in *Dapedium* and *Paradapedium*.

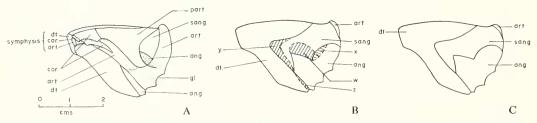
There is only a slight rib-like thickening along the row of scales on the belly in *Dapedium* and *Paradapedium*. The flank and belly scales in *Paradapedium* are, however, more elongate than *Dapedium*. The dorsal ridge scales are not very conspicuous in *Dapedium*. In *Paradapedium* there is a slight individual variation but the same are usually a little more conspicuous than *Dapedium* and are pectinate or slightly denticulate. The neural spines are fused to the respective arches throughout the length of the body in *Paradapedium* but in *Dapedium* these are fused only in the hinder part of the body. The dorsal and anal fin in *Dapedium* have been shown in Woodward's (1895) reconstruction to have 28 and 17 fin rays respectively. *Paradapedium* (ISI P. 34) has 35 and 25 fins, respectively, in dorsal and anal fins.





TEXT-FIG. 9. *Dapedium punctatum* (BMNH 36883), mesial view of right lower jaw and palate.

TEXT-FIG. 10. *Dapedium* sp. (BMNH P. 4877), mesial view of right lower jaw.



TEXT-FIG. 11. Restoration of lower jaw of *Dapedium* sp. (from BMNH P. 4877). A, internal view; B, mesial view; C, external view. (Teeth and lateral lines omitted; areas of overlap hatched.) w, surangular-angular overlap, surangular lying external to angular; x, angular-surangular overlap, angular lying external to surangular; y, surangular-dentary overlap, surangular lying external to dentary; z, dentary-angular overlap, dentary lying external to angular.

TETRAGONOLEPIS

Three species of *Tetragonolepis* have been described from the Kota formation by Egerton (1878), namely, *T. oldhami*, *T. rugosus*, and *T. analis* on the basis of 5 specimens. Only three specimens of *Tetragonolepis* are traceable in the collections of GSI, Calcutta, in addition to the newly collected material in GSU, ISI. One specimen each of the GSI collection is assignable to the 3 species of *Tetragonolepis* on the basis of Egerton's figures, though no holotypes had been designated by Egerton. As such each of the specimens can be designated as a lectotype of the respective species: *T. oldhami*—lectotype GSI 2145 (Egerton 1878, pl. II, fig. 1); *T. rugosus*—lectotype GSI 2146 (Egerton 1878, pl. II, fig. 2); and *T. analis*—lectotype GSI 2150 (Egerton 1878, pl. III, fig. 1). Woodward (1895, p. 161) considered the Indian species of *Tetragonolepis*. He recognized *T. oldhami* and gave a diagnosis of this species but listed *T. analis* and *T. rugosus* as based upon fragmentary specimens. A re-examination of the species of *Tetragonolepis* from India was done on the basis of collections in GSI and the newly collected material in the light of a new diagnosis by Gardiner (1960).

SYSTEMATIC DESCRIPTION

Genus Tetragonolepis

Type species. Tetragouolepis semicincta Bronn 1830, from the Upper Lias (Lower Jurassic), Wurtemburg and Bavaria (West Germany).

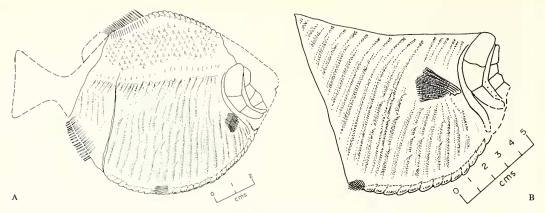
Diagnosis of genus. As given by Gardiner (1960, p. 305) except the number of suborbitals which may be 3 to 4.

Tetragonolepis oldhami Egerton Plate 15; text-figs. 12 and 13

Diagnosis. Tetragonolepis attaining an estimated length up to 180 mm, with abdominal protuberance about twice that of the portion above the lateral line canal. Branchiostegal rays, 3, elongated, progressively larger starting from the anterior one. Preopercular angulate, slightly or markedly. Suborbitals 4, asymmetric. Caudal fin has 15–16 haemal arches supporting lower lobe.

Distribution. Lower Jurassic, India; Kota formation.

Lectotype. GSI 2145 is preserved entirely as an impression (Egerton 1878, pl. II, fig. 1; redrawn here, text-fig. 12A). It has most of the trunk including the region of dorsal and ventral ridge scales, parts of dorsal and anal fin, but lacks the caudal fin. The anterior and dorsal portion of the skull is missing. The body is clearly hypsisomid; about twice as deep below the central axis than above it. The preserved portion is about 92 mm long. It is estimated that the fish was about 128 mm long. Nothing can be ascertained about dermal skull pattern, snout, and jaws. Four suborbitals are recognizable which are asymmetric. The preopercular is somewhat angulate and the opercular is deep (approx. length/width ratio 2:1). The interopercular is slightly deeper than subopercular. The cleithrum is sigmoid. The portion of the body below

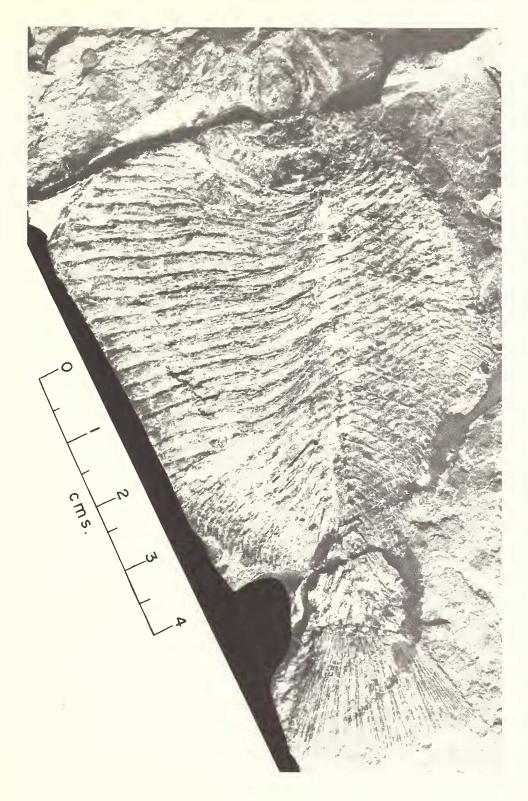


TEXT-FIG. 12. *Tetragonolepis oldhami*: A, lectotype (GSI 2145), with restored outlines; B, ISI P. 36, complete specimen, preserved as impression.

the central axis displays prominent haemal arches and ribs. There are indications of strong ribs. The scales appear to have been much deeper below the central axis than above it. The ventral ridge scales are more conspicuous than dorsal and bear fine pectinations at the ridges. The pectoral fin originates at the level of subopercular-interopercular suture and has 12–14 lepidotrichia. The pelvic fin is vestigeal and has 6–7 lepidotrichia. The dorsal fin is preserved only anteriorly but has about 16 lepidotrichia, supported by an equal number of radials. The lepidotrichia were probably segmented and distally bifurcated. The anal fin is preserved anteriorly and has 17–18 close-set lepidotrichia with equal member of radials.

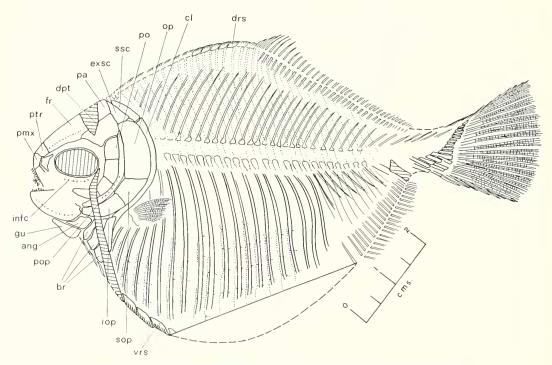
Material. Lectotype (GSI 2145), Kota formation, India, fish wanting anterior and dorsal portion of head and tail, about 92 mm long and 88 mm deep. New specimens: ISI P. 36, Kota ledge (near village Kota: text-fig. 2), Kota formation, India, fragment of ventral part of the trunk and posterior region of head preserved as an impression, 120 mm long and 90 mm deep. ISI P. 37 and 37*a*, Kota limestone near Lingal-Metpalli (text-fig. 2), Kota formation, India, nearly complete fish, part, and counterpart, 108 mm long and 65 mm deep.

Description. Tetragonolepis oldhami is a moderately sized semionotid reaching an estimated length of 108–180 mm and depth of 65–130 mm as seen from the lectotype and new specimens. The dermal bones of the skull in ISI P. 37 form a head shield in which the sutures are close set (Pl. 15 and text-fig. 13). The suture between frontal and parietal is obscured but the suture between dermopterotic and frontal and dermopterotic and parietal is visible. The dermopterotic is larger than the parietal. The head shield has a fine tubercular ornamentation. 4 suborbitals are seen in ISI P. 36 and 37 (text-figs. 12B and 13), similar to the lectotype. The antorbital was probably triangular and the post-rostral squarish (text-fig. 13). The nasal is uncertain.



The premaxilla is displaced slightly and the shape of the maxilla cannot be determined posteriorly. There are fine, pointed teeth on premaxilla, maxilla, and palate. The circumorbitals could not be determined but in ISI P. 37 (text-fig. 13) the orbit seems to be surrounded by a sclerotic ring. The infraorbital sensory canal can be seen ventrally below the orbit. The lower jaw (text-fig. 13) is deep but is vague dorsally. The dentary is large, bearing fine, pointed teeth, similar to those on premaxilla and maxilla. The angular is displaced and can be seen partly behind the dentary. The mandibular sensory canal is visible. Between the rami of the lower jaw there is a gular plate. Three branchiostegal rays are seen, becoming progressively longer from the anterior. The opercular apparatus is visible in all specimens. The preopercular has a clearly ascending process and is angulate. The opercular and interopercular are both deeper than the subopercular. The cleithrum is characteristically sigmoid and an elongated suprascapular is present.

The body is covered with scales each of which has a sharply thickened rib on its anterior border. The scales are small and rhombic on the dorsal side of the notochordal axis and quadrangular and deep on the ventral side. There are 10–11 horizontal rows in the dorsal region and 8–9 in the ventral region of the body. The dorsal and ventral ridge scales bear fine pectinations and serrations but the former are only half as big as the latter (text-fig. 13). The neural spines are fused to the supporting arches along the length of the body but do not reach the body margin. The haemal spines are shorter. An 'inner' rib (text-fig. 13) is present in the flank and belly region.



TEXT-FIG. 13. Tetragonolepis oldhami, from ISI P. 37 and a, complete specimen.

The pectoral fin is delicate (text-figs. 12 and 13) and made up of about 10–11 lepidotrichia. The pelvic fin is vestigial (text-figs. 12A and B) and is made up of about 6–7 lepidotrichia. The dorsal fin stretches from the dorsal apex of the body almost to the tail and has the same number of radials as lepidotrichia, of which 34 can be counted in the dorsal fin of ISI P. 37 (text-fig. 13). The anal fin is not preserved completely in any specimen but it is less extensive than the dorsal fin. The anal fin has between 20 and 25 lepidotrichia and the same number of radials. The caudal fin is preserved only in ISI P. 37 (text-fig. 13) and has 15–16 haemal spines supporting the lower lobe. The lepidotrichia are segmented and distally bifurcated. There are fringing fulcra on the fin both dorsally and ventrally.

Discussion. The body proportions and characteristics of T. *oldhami* such as the number and disposition of suborbitals, arrangement of opercular apparatus, characteristic shape of cleithrum, presence of robust ribs in the body, and the disposition of median and paired fins are more or less identical in all specimens.

Tetragonolepis is essentially a European Liassic genus apart from these Indian representatives. The proportions of the body, number, and disposition of suborbitals and the shape of preoperculum are some of the important characteristics in which *T. oldhami* is distinguishable from *T. semicincta* (Upper Lias: Wurtemberg and Bavaria, W. Germany), *T. discus* (Upper Lias: Gloucestershire, England), and *T. drosera* (Upper Lias: Wurtemberg, W. Germany).

Two other species of *Tetragonolepis* from the Kota formation were proposed by Egerton (1878), *T. rugosus* and *T. analis. T. rugosus* is represented by a single fragmentary specimen (lectotype GSI 2146) which is about 70 mm across (Egerton 1878, pl. II, fig. 2). This shows a group of scales from the anterior region of body as impressions which suggest a 'rugged coat of ganoine, almost tubercular in aspect'. This single character of scales led Egerton to erect a new species of *Tetragonolepis*. The specimen is too fragmentary to exhibit any diagnostic characteristic of the genus *Tetragonolepis* and as such it should be regarded as *sp. indet. T. analis* is also represented by a single specimen (lectotype GSI 2150). The other two specimes ('portions of two other fish' mentioned by Egerton) have since been lost. The lectotype is well illustrated (Egerton 1878, pl. III, fig. 1) and is almost entirely preserved as an impression. This is clearly a deep-bodied form. Unfortunately, however, only the rear of the head is seen so that nothing is known about the dermal skull pattern nor is certain information obtainable on the opercular series. There seems to be 2–3 enlarged branchiostegal rays but their outlines cannot be clearly seen. The cleithrum is probably sigmoid. The pectoral fin is not seen. The pelvic fin is vestigial, having 7–8 lepidotrichia. The anterior part of the anal fin is preserved having lepidotrichia which are bifurcated and distally segmented. There appears to have been a complete covering of scales on the body. The scales below the notochordal axis are deeper than those above it. The proportions, however, cannot be worked out as the dorsal region of the body is missing. Thus the lectotype of *T. analis* exhibits certain characteristic suggesting a deep-bodied fish but not distinctive enough to be recognized as a species of *Tetragonolepis*. As such *T. analis* should be regarded as *sp. indet*. It may be mentioned that Woodward (1895, p. 162) classified the two species, *T. rugosus* and *T. analis*

AGE AND DISTRIBUTION OF THE HYPSISOMID SEMIONOTIDS

The semionotids are mostly fusiform to hypsisomid fishes with small mouths (Schaeffer 1967). There are two evolutionary trends from a basic form, typified by *Semionotus* and *Acentrophorus*, which on the one hand have given rise to hypsisomid forms such as *Dapedium* and *Tetragonolepis* and on the other hand produced the fusiform *Lepidotes*. Lehman (1966) has subdivided semionotids, on the basis of body shape, restricting the fusiform semionotids to the family Semionotidae (except *Lepisosteus*, which is placed in a new order Lepisosteiformes) and the hypsisomid forms to a new family Dapediidae. He has included *Dapedium*, *Tetragonolepis*, *Heterostrophus*, and *Dandya* in the family Dapediidae. Schaeffer (1967) has erected the genus *Hemicalypterus*, and another genus, *Paradapedium*, is proposed in this paper, both being hypsisomid. Thus 6 genera of hypsisomid semionotids are known:

1. Hemicalypterus Schaeffer 1967. Chinle formation, Upper Triassic, North America.

2. Dandya White and Moy-Thomas 1940. Upper Triassic, Hallein, Austria.

3. *Tetragonolepis* Bronn 1830. Upper Lias. Wurtemberg and Bavaria, West Germany, and Gloucestershire, England; Kota formation, Lower Jurassic, India.

4. *Dapedium* Leach 1822. Lower Lias, Lyme Regis, England, and Alsace, Germany; Upper Lias, Yonne (Vassy), Normandy, France, and Wurtemburg, Germany.

5. *Heterostrophus* Wagner 1863. Oxfordian, England, and Lower Kimmeridgian (= Solenhofen) of Germany.

6. Paradapedium Jain 1973. Kota formation, Lower Jurassic, Deccan, India.

Schaeffer (1967) does not support the inclusion of *Heterostrophus* and *Dandya* in the family Dapediidae. *Heterostrophus* has been restudied by Woodward (1929) and is known by a single specimen from Solenhofen, Bavaria (*H. latus*). There is also fragmentary evidence of a similar fish from the Oxford Clay of Peterborough, England (*H. phillipsi*). *Heterostrophus* has close resemblance to *Dapedium* in many features of the skull. The body is known only in *H. latus* which is not hypsisomid. *Dandya* is represented by a single neurocranium and some anterior body scales. It is not certain (Lehman 1966) that it belongs to the family Dapediidae. The present author supports Schaeffer's views in not including these genera in the family Dapediidae. The remaining four hypsisomid genera of the Semionotidae (excluding *Heterostrophus* and *Daudya*) are known by a number of well-preserved specimens. Table 1 shows a comparison of these genera.

The distribution in time and space of *Hemicalypterus*, *Dapedium*, *Tetragonolepis*, and *Paradapedium* reveals the following: *Hemicalypterus* is the earliest hypsisomid semionotid and is restricted to the Upper Triassic; *Dapedium* is known from Lower and Upper Lias; *Tetragonolepis* is restricted to the Upper Lias; *Paradapedium* is similar to *Dapedium*, and is known with *Tetragonolepis* from India. It seems, therefore, that *Paradapedium* may be an ecological substitute for *Dapedium* in Asia, and need not necessarily be younger or older than *Dapedium*.

The hypsisomid semionotids do not occur in horizons lower than Upper Triassic and higher than Liassic, i.e. Lower Jurassic. *Hemicalypterus* (Upper Triassic) is distinctive from the Liassic hypsisomid semionotids of Europe and India, but the latter show close resemblance among themselves. It seems unlikely, therefore, that the Kota formation is younger than the Lower Jurassic, and the evidence favours

Hemicalypterus	?50% (Schaeffer's restor- ation)	39% (Schaeffer's restora- tion)	30% (Schaeffer's restora- tion)	Posterior half of body naked; scales deeper in mid body	Much enlarged and pro- minent; strongly denti- culate	Thin and delicate; feeble ornamentation	3; slightly extending be- vond mid orbit	2	Not known	Not known	Not completely known	Similar in size	? Arched	? Fused with neural arch throughout the length of body
Tetragonolepis	60% (T. oldhami; 1 speci- men)	30% (T. oldhami; 1 speci- men)	28% (T. oldhami; 1 speci- men)	Full body; scales deeper in belly	Ventral larger than dorsal, both serrated	Thin, feebly ornamented	3-4; not extending be- yond mid orbit	1	Not known	Not known	Like Dapedium in shape	Similar in size	Sigmoid	Fused with neural arch throughout the length of body
Paradapedium	70-72% (2 specimens)	15% (1 specimen)	16% (l specimen)	Full body; scales deeper than Dapedium in belly	Dorsal and ventral slightly more conspicuous than <i>Dapedium</i> ; pectinate or denticulate	Not heavily ossified; deli- cate ornament	9-10; extending beyond mid orbit	3	Slender and delicate: fora- men (VII) at about mid length	? Triangular, moderate; poorly defined articula- tion facet	More definitely V-shaped	Anterior tooth enlarged	Arched	Fused with neural arch throughout the length of body
Dapedium	60-65% (4 species; 15 specimens)	26-34% (3 species; 13 specimens)	33-40% (3 species; 12 specimens)	Full body; scales deeper in belly	Dorsal, pectinate, or den- ticulate: ventral, more prominent than dorsal	Heavily ossified; tubercu- lated	6-11; not extending be- yond mid orbit	4-6	Stout; foramen (VII) above mid length	Squarish; stout; prominent articulation facet	Like open V	Similar in size	Arched	Fused with neural arch in hinder part of body only
Body proportions:	a. Depth of body below lateral line canal as percentage of total body depth	b. Length of head as percentage of body length	c. Depth of head as percentage of body length	Body squamation	Ridge scales	Head bones	Suborbitals	Extrascapulars	Hyomandibular	Quadrate	Dentary	Dentary teeth	Cleithrum	Neural spines

TABLE 1. Comparison of characteristics of hypsisomid semionotids

JAIN: JURASSIC FISH FROM INDIA

175

a Lower to Upper Liassic age. *Hemicalypterus* is known only from a continental formation. *Dapedium* occurs in marine sediments but a rather similar genus *Para-dapedium* is found in continental beds. *Tetragonolepis* is known from marine sediments in Europe and fresh-water habitats in India. It is, therefore, likely that they were euryhaline forms. Schaeffer (1967) has suggested that these fishes probably assumed ecological roles similar to certain species of *Cyprinodon*, the centrarchids and the characins. *Tetragonolepis* and *Dapedium* are known from the northern margins of Tethys. In addition, *Tetragonolepis* also occurs in a continental area south of Tethys, i.e. India. *Paradapedium* is known from south of Tethys. *Hemicalypterus* occurs in the continental land mass of North America, presumably northwest of Tethys. The deep-bodied semionotids seem, therefore, to be enjoying a cosmopolitan distribution on both sides of Tethys over a rather limited span of time—the Later Triassic and Early Jurassic.

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LIST OF ABBREVIATIONS USED IN TEXT-FIGURES

ang.-angular ao.-antorbital art.-articular art. prop.-articulation facet for preopercular aut.-autopalatine br.-branchiostegal ray cl.-cleithrum co.—circumorbital cor.-coronoid dermp.-dermopalatine dpt.-dermopterotic drs.-dorsal ridge scales dt.-dentary dt.t.-dentary teeth ectpt.-ectopterygoid enpt.-entopterygoid exsc.-extrascapular fr.-frontal gl.-glenoid fossa gu.—gular hym.-hyomandibular hym. f.-hyomandibular foramen iop.-interopercular info.—infraorbital infc.-infraorbital sensory canal

l.l.j.-left lower jaw m.c.-mandibular canal mtpt.-metapterygoid mx.—maxilla na.—nasal nar.—naris op.-opercular op. pr.-opercular process pa.-parietal part.-prearticular pect. f.-pectoral fin pmx.-premaxilla pmx. t.-premaxillary tooth po.-postorbital pop.-preopercular ptr.-post-rostral qu.—quadrate r.l.j.-right lower jaw ros.-rostral sang.-surangular so.-suborbital sop.-subopercular ssc.—suprascapular sym.-symplectic vrs.-ventral ridge scales

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